Benthic-pelagic coupling

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CHAPTER 7

• Summary and concluding remarks •

7.1. Thesis summary

In this thesis, various aspects of benthic-pelagic coupling and the organic matter in the near-bottom seston and the sediments of the North Sea are described. Chapter 2 and 3 focus on the short-term, seasonal and spatial differences in the amount and composition of near-bottom seston in the south, south-east and north-east of the North Sea. In the fourth and fifth chapter, the concentration and quality of phytodetritus in near-bottom water and sediments in non-depositional areas in the southern North Sea are depicted in relation to benthic metabolism. The sixth chapter extends the study in chapters 4 and 5 to depositional regions in the south-east and north-east of the North Sea, using an additional set of biomarkers for the origin and quality of the sedimentary organic matter and for benthic metabolism.

The choice for these stations was based on earlier studies, which demonstrated that these sites differed conspicuously in sediment type, nutrient fluxes and benthic community biomass and composition. To what extent these stations are representative of the area they are located in (and from which their name is derived), is uncertain. More detailed studies have illustrated the high variation in benthic environments within these areas. Of course, such a diversity can not be covered by the stations used in this study.

The two studies on the near-bottom seston (chapter 2 and 3) were performed using a sediment trap at 3 meter above the seafloor and a sediment recorder placed on the sediment. This recorder consists of a flat, 5 cm high disk with a diameter of 1 m. By opening a small, 1 cm deep cup in the centre on the top side of the disk, material was sampled from the lowest near-bottom water layer. These studies showed that characteristic temporal (seasonal, tidal) and spatial differences exist between the amount and nature of the particulate matter in the near-bottom water layer of the North Sea.

Hydrographic factors plays a crucial role in the amount and nature of near-bottom seston. The relation with sediment type is also evident. At the Broad Fourteens (BF), the sediment consists largely of medium coarse and fine sand, with low percentages of organic carbon. In combination with relatively high near-bottom water (nbw) current velocities, this results in higher total particulate matter fluxes to the traps than at the Frisian Front (FF). The seston at BF was mainly made up of fine sand with low organic content, while at FF it consisted of fine, silty particles with a higher organic matter concentration than at BF. However, the organic matter at BF is of higher quality, *i.e.* contains more chlorophyll *a* and polyunsaturated fatty acids than that at FF. This suggests that the near-bottom seston at FF is relatively enriched with resuspended refractory carbon from the sediment top layer. Laboratory studies and field observations have demonstrated that such differences in near-bottom organic matter concentrations and quality have an effect on the activity and growth of animals feeding on this material. This explains the higher growth rates of the sea urchin *Echinocardium cordatum* at BF than of those at FF (Duineveld & Jenness 1984). The effect of the algal spring bloom is reflected in the near-bottom seston composition. More algal detritus is notable in samples taken in the spring than in those from other periods. Furthermore, large differences in trap fluxes and composition were found within tidal cycles at BF and FF The data indicate an aggregating role of sedimented algae in the resuspension of bottom material. Estimations indicate that the majority of the samples consisted of resuspended matter, with a larger fraction resuspended material in de recorder than in de trap. In addition, the near-bottom samples from BF contain more resuspended matter than those from FF.

The effect of hydrographic factors was also evident at the depositional areas in the North Sea, namely the German Bight and the Skagerrak. The German Bight (GB) is characterised by current velocities comparable to those at BF. However, since its sediments are siltier than those at BF are, the amount of carbon trapped here is more than an order of magnitude higher. Furthermore, the terrestrial signature (long-chain fatty acids) of the near-bottom seston was highest in the German Bight, likely as a result of the input of particulate organic matter by the Elbe and Weser rivers. The amount of organic carbon trapped at the location in the Skagerrak (SK), characterised by relatively low nbw current velocities, was low compared to the other stations. The organic matter in the near-bottom seston at this station was more degraded than that at the other stations, but not as refractory as implied by earlier studies. Although the near-bottom samples were taken during short time intervals (12 hours in February and May), which might have resulted in missing pulses of particulate mater, these data do not indicate an important input of terrestrial or highly refractory organic matter as has been suggested earlier for this area (Liebezeit 1987, Anton *et al.* 1993).

The seasonal input of phytodetritus in near-bottom water and sediments is well illustrated by the studies performed during February, March, May, June, August and November 1993 at three stations in the southern North Sea (chapters 4 and 5). Phytopigment analyses on the near-bottom water samples showed a succession in the amount and the origin of phytodetritus. Early in the year, diatoms were important at all three stations. A clear change occurred in May, during the spring bloom when the flagellate *Phaeocystis* sp. became the most prominent algal species in the surface and near-bottom water at all three stations. In the summer and autumn, the succession at the three stations diverged. At BF, with a constantly mixed water column, green algae (prasinophytes) dominated. At the Oyster Ground, with a layered water column, dinoflagellates were the most important species. A mixture of these two groups was noted at the Frisian Front.

The concentrations of chlorophyll a in the sediment reflected well the quantitative succession in the water column, and showed the spring bloom sedimentation even better than the water samples. The Frisian Front showed the highest concentrations of algal detritus in the sediment, while sediments at BF contained the lowest amount. The sediment oxygen consumption (SOD) at BF and FF increased as a reaction to the spring input of phytodetritus, and continued to climb concurrently with the nbw temperature in the summer and autumn. At BF, the SOD declined earlier (mid-summer) than at FF (autumn), probably due to limited food supply after the spring bloom, which was not the case at FF. Here, the SOD reached its maximum in August/September.

The growth of a small deposit-feeding bivalve, *Mysella bidentata*, showed its maximum shortly after the spring bloom, while during mid-summer and autumn, hardly any growth was noted. This temporal uncoupling of bivalve growth and whole community (mainly by bacteria) respiration is probably an adaptation of the bivalve to the timed arrival of its food source. It is known that algae contain essential components, like polyunsaturated fatty acids, for the growth and reproduction of most animals. Hence, they are in the advantage when feeding on fresh algal detritus early in the year, when temperatures and thus bacterial competition are low.

To see whether also the physical activity of benthos varied with the input of detritus, we calculated bioturbation from the profiles of chlorophyll a in the sediments at BF, FF and OG (Oyster Ground). Only at BF, there was a positive relation between these two parameters. The other stations suggested a trend (FF) or no relation at all (OG). It became clear that variation in sedimentary concentrations and profiles of chlorophyll *a* between replicates of a station is quite large, strongly affecting significance of the differences in bioturbation between the stations and months. The same holds for the fluxes of chlorophyll *a* to the sediment, which were calculated with the same model that generated the bioturbation rates, and indicated the highest fluxes to the sediment at FF and in May.

When the fluxes of chlorophyll *a* and the sediment oxygen demands were converted into carbon units, a benthic carbon budget could be calculated for the three stations. The results indicate that in springtime more carbon is supplied than remineralised, while the reverse is found in late summer or autumn. This suggests that in springtime a labile carbon pool is built up, which is degraded later in the summer and the autumn. Since the annual budgets were reasonably (BF) to very well balanced (FF and OG), this indicates that chlorophyll *a* is good marker for the input of metabolisable organic carbon to sediments.

A comparison of benthic-pelagic coupling at non-depositional sites (southern North Sea) and depositional sites (German Bight and Skagerrak) was described in chapter 6. Next to the use of chlorophyll *a* and breakdown products, the sedimentary detritus was also described by its fatty acid composition. Furthermore, besides the sediment oxygen demand, bulk RNA and DNA in the sediment was used as an additional metabolic parameter for the benthic community. Both fatty acids and chlorophyll *a* indicated a trend in phytodetritus settlement comparable to that in earlier studies, with an exception for the Skagerrak station. The sediment at the depositional locations contained higher concentrations of phytodetritus than that at the two non-depositional stations BF and FF in the southern North Sea. This study confirmed other studies on benthic nutrient fluxes in the German Bight (*e.g.* Lohse *et al.* 1995), which suggested that this area receives a relatively large amount of labile organic matter. The variations in metabolic indices, the SOD and the RNA and DNA content of the sediment, were congruent with the inventories of labile organic matter at all stations, except the Skagerrak. The fatty acid analyses showed that the sedimentary organic matter at GB, and to a lesser extent also at SK, was relatively enriched in long-chain fatty acids, possibly with a terrestrial origin. These sediments also contained higher concentrations of bacterial fatty acids, likely related to the higher proportions of fine sedimentary particles here in comparison to the sediment at BF and FF.

Surprisingly, the Skagerrak station contained comparable or even higher amounts of sedimentary phytodetritus than GB. This was not expected, taking into account the depth at SK (270 m) and earlier studies which indicated the predominantly refractory and terrestrial nature of sedimentary organic matter (Liebezeit 1987, Anton *et al.* 1993, De Haas 1997). The relatively high concentrations of RNA presumed to be active and largely with a bacterial origin, indicated a high metabolism. However, neither the SOD nor the conjointly measured nutrient fluxes and sulphate-reduction rates (Van der Zee, pers. comm.) indicated high aerobic or anaerobic metabolism. A lower nbw temperature only partly explains the decreased SOD. It is hypothesised that some sort of protection to degradation, possibly adsorption of labile organic matter to clayey sediment as proposed by Keil *et al.* (1994) and Ransom *et al.* (1997), is responsible for the lower metabolic rates. A comparable mechanism might explain the relatively too high RNA concentrations.

Lastly, our studies have shown that chlorophyll *a* and polyunsaturated fatty acids (pufas) are well correlated, both in sediment and in near-bottom seston, pointing at comparable degradation rates. This is important because these pufas are essential components for most, if not all animals. They lack the biosynthetic pathways to produce these compounds, while pufas perform crucial functions in organisms. It has been demonstrated that they limit the growth and reproduction of heterotrophs if not present in the available organic matter. As such, chlorophyll *a* is also a marker for the quality of organic matter as a food source for benthic metazoans.

7.2. Reflections and future outlook

Benthic-pelagic coupling as defined in chapter 1 and studied in this thesis is one of several approaches to do research on the functioning and structure of benthic ecosystems. It focuses on the relatively large-scale processes and pertains to the question of the variation in activity and biomass of benthic communities throughout the North Sea. The organisms mediating the marine organic matter cycle are treated more or less as black boxes. In my opinion, this kind of knowledge of benthic ecosystems should form the basis for our understanding of the structure and functioning of benthic ecosystems, *viz.* it is the context from which studies on relatively small-scale events start. To know why and where we find which organisms, many more questions need to be answered, especially at the population and organism level.

The role of individual species and organisms groups on the cycling of organic matter is largely unknown. The direct contribution of macrobenthos and meiobenthos to total benthic metabolism is still estimated from their size-distribution, using a biomass-activity conversion factor. Only few studies have been performed on their indirect contribution to whole community activity, through stimulation of the bacterial population (bioturbation, bio-irrigation, defecation, ammonia secretion). Nowadays, benthic lander technology is developed up to a point where it is possible to perform experiments within an *in-situ* chamber on the seafloor. Such a field experiment could consist of the supply of *e.g.* labelled organic matter to the sediment and measure the, depth-distributed, changes in community metabolism with high-technology probes within the sediment. Afterwards, the sediment core could be removed to measure the down-core distribution of labelled detritus and the content of the label within the benthic animals and bacteria. This would disclose the contribution of the organism groups to the organic matter cycling and the total of metabolic activity, as well as the fate of fresh organic matter in the sediment.

Another likely factor contributing to the diversity and activity of benthic communities is the natural (spatial) heterogeneity in the amount and quality of detritus settling to and present in sediments. Crassous & Khripounoff (1994) showed that a large variation exists in the sedimentation of settling material near the sediment surface on various scales, from several metres to kilometres. Such heterogeneity also exists concerning the concentrations of labile organic matter in sediments (chapter 4, 5; Van Duyl *et al.* 1997). Hence, finding a high variation in the organic compound concentrations in sediments and water is a problem inherent to fieldwork. Because of this high variation, it is sometimes hard to find significant differences between stations or months on the concentrations of detritus. One is forced merely to speak in terms of trends, instead of higher or lower , and a frequent advice from manuscript referees is why not more samples were taken. A question is then, how many samples are needed to get a (better) significance in the data found in these studies: 3, 10 or 20? Heterogeneity in organic matter concentrations is characteristic for natural environments, and the only reason for wanting significance is the assumption that a certain sample is representative for the area it comes from. Due to the large spatial variability in benthic characteristics, this assertion is questionable. Nevertheless, the sample is representative for its exact location, and any variation is due to some process and not the result of some random movement of particles in the water or sediment. Although this does not mean that statistic analysis of data is worthless, it does suggest that more attention should be paid to the mechanisms underlying natural heterogeneity of data, even at small scales, rather than just stating the insignificance. The fact that some differences are insignificant does not mean that they are trivial, *i.e.* that they do not mean anything. Plante *et al.* (1986) showed a high heterogeneity in coastal sedimentary pigments, and how this affects sampling strategies. If their guidelines are followed, one would certainly need to spend much more time on sampling (and consequently also on analyses) than is usually done. It might be assumed that the above mentioned heterogeneity contributes importantly to the diversity in the number and biomass of benthic organisms. Furthermore, to what extent this variation drives the competition for a common food source between and within species has not been studied in subtidal benthic communities. Deposit feeding, suspension feeding, bacterivory, predation, the spectrum of feeding strategies of benthic animals is well acknowledged. But their performance and flexibility under varying circumstances, as well as the limits of their capabilities to handle strong near-bottom currents and food competition and to survive food-deprived periods is still as clear as the mud they are living in.

Studies like these strongly relate to the dynamic character of ecosystems. Often marine ecological researchers are forced to take snap-shots of an ecosystem. Although it is commonly realised that living systems are not in a steady state, many studies necessarily assume it to facilitate modelling or calculations like those in chapter 5. Admittedly, dynamical modelling requires quantitative relationships between organisms and/or organisms and their food source, many of which have not yet been defined. Such relationships are not easily obtained from benthic ecosystems. To this goal, certain model species should be selected, of which the food preferences, eco-physiology and life history parameters should be obtained. Choosing a model organism is not an easy task, because a balance should be found between practicality and specificity. The model organism should be present in a variety of habitats, so that its adaptations to important factors like hydrography and sediment type can be studied. Obviously, the organism should not be too non-specific regarding such factors. Other criteria could be its size, anatomical complexity and sensitivity to handling. A relatively large size and low anatomical complexity are preferred because then it is easy to dissect the animal and to study its physiology, like digestion and assimilation of food components. Its sensitivity to handling is relevant in order to perform laboratory experiments. Ultimately, every species will have its drawbacks, and it will be necessary to use more than one organism. The deposit-feeding heart urchin *Echinocardium cordatum* could well be such a model organism. It is an important species in a variety of benthic habitats in the North Sea, from the sandy Broad Fourteens to the muddy German Bight. It can easily be dissected, and has a simple anatomy. When sampled with a box corer, it can be transported without damage to the laboratory, for use in mesocosm experiments. Due to its size and foraging activity, it contributes significantly to bioturbation in the sediment. As such, it forms an important species in the benthic food web. The anatomy and morphology of the organism are relatively well studied, and the animal has been used in several laboratory experiments. Its main drawback is that it does not feed from the suspended matter in the near-bottom water layer, and hence it is not very sensitive to hydrography. To this extent, the filter-feeding bivalve *Arctica islandica* is a good candidate. Studies at the NIOZ have shown that this species can be grown in the laboratory. It is relatively large, and an important species in the central and northern North Sea, occurring in a variety of habitats.

Subsequently, chemical analyses on the organic matter in water and sediment as a food source, and on the tissues of the benthic animals need to form an integral part of benthic ecological studies. In my opinion, phytopigments, lipid classes, fatty acids and naturally occurring isotopes are the most important compounds when studying both ecosystem processes and individual organisms. Since in most cases the ultimate food source for benthic organisms is the algal detritus, phytopigments can disclose the amount and quality of the available food. The use of lipids in ecological studies has many advantages. They are not only marker substances, like phytopigments, but are also an important part of animal tissue, and crucial compounds in the functioning and survival of organisms. Two important lipid classes are the phospholipids and the neutral lipids. The first class forms a structural part of cell membranes, and usually contains a large concentration of polyunsaturated fatty acids in order to keep the cell membrane fluid at low temperatures. Since most animals do not have the ability to synthesise these components, they have to be derived from their food, the algal detritus. Hence, their phospholipid fatty acid composition displays the need of an animal for a certain quality of its food. The other main lipid class is the neutral lipids, mainly consisting of glycerides and wax esters, and largely forming the long-term energy storage components. The fatty acid composition of these lipids has demonstrated to reflect the food source of the organism in question. The relevance of algal detritus or bacterial biomass, each with their specific fatty acids, as a food source for an organism can thus be revealed. In this way, the organism can be given a place in the food web, its contribution to organic matter degradation or transformation can be illustrated, and the assimilation of food by the organism can be disclosed. Additionally, the use of natural isotopes (of C, N and O), especially in combination with lipid analyses, can give additional information on the source of organic matter, whether or not ingested and assimilated by animals. Recent studies clearly have indicated the usefulness of this approach, and demonstrated its potency for ecological research (Kharlamenko *et al.* 1995, St. John & Lund 1996, Pond *et al.* 1997).

Lastly, the recent developments in molecular ecology should be extended to the field of benthic ecology. Bulk RNA and DNA analyses are useful up to a certain level, and in chapter 6 the possible advantages and drawbacks have been discussed. A higher resolution on the genetic molecular level is certainly desirable, and nowadays also feasible. Although an appropriate method to extract nucleic acids from sediments still is a matter of discussion, it will only be a matter of time before this is settled. The probing of RNA as well as DNA, followed by quantitative hybridisation will generate results revealing the (bacterial, protozoan and metazoan) biomass and activity in sediments. With the ongoing increase in analytical speed and sensitivity, it can be foreseen that in the near future such analyses will become a standard.

Another major application of these molecular techniques might be in recruitment studies, *i.e.* on the distribution, settlement and survival of pelagic larvae of benthic animals. The classical research technique, using binocular or microscope to identify and count larvae is hugely time-consuming. In addition, the identification of subgroups within the distribution of a benthic animal species can be an important employment of this technique. As Witbaard *et al.* (1994) have shown, various populations of *Arctica islandica* show different growth rates at different locations in the North Sea. One question is whether such differences are caused by a difference in genetic composition of the *Arctica* populations, and if there is any exchange of genetic information between these populations.

This paragraph on suggestions for possible future research is certainly not exhaustive. It does however indicate that there is a growing need to be able to go beyond the boundaries of one s own discipline. The interdisciplinary approach, where co-operating scientists are able to engage in new approaches, is essential for a further development of the marine ecological sciences. Closely related to this, it is commonly acknowledged that one fool can raise more questions than ten wise men (f/m) can answer. It is thus questionable whether the tendency of more society-based research will benefit the objectivity and productivity of the scientific practice.